

Appendix A Response of susceptible density to parameter changes drives change in CSS trait value.

The equation for the location of the singularity is,

$$\left. \frac{\partial r}{\partial \beta} \right|_{\bar{\beta}=\beta=\beta^*} = (X - \alpha'(\bar{\beta})(1 + cH)) \Big|_{\bar{\beta}=\beta=\beta^*} = 0, \quad (\text{A.1})$$

where the invasion fitness, r , is given by equation (5) - *main text*. The infecteds ODE is,

$$\frac{dY}{dt} = \beta XY - (\alpha(1 + cH) + b + \gamma)Y. \quad (\text{A.2})$$

Differentiating equation (A.1) with respect to the strength of DDV , c , combining with equilibrium total host density from equation (A.2), its derivative with respect to c , and equation (A.1) leads to,

$$\left. \frac{\partial}{\partial c} \frac{\partial \alpha}{\partial \bar{\beta}} \right|_{\bar{\beta}=\beta=\beta^*} = - \left. \frac{\partial X}{\partial c} \frac{(b + \gamma)}{\alpha(1 + cH)^2} \right|_{\bar{\beta}=\beta=\beta^*}, \quad (\text{A.3})$$

analogously,

$$\frac{\partial}{\partial a} \frac{\partial \alpha}{\partial \bar{\beta}} = - \frac{\partial X}{\partial a} \frac{(b + \gamma)}{\alpha(1 + cH)^2} \quad (\text{A.4})$$

$$\frac{\partial}{\partial \mu} \frac{\partial \alpha}{\partial \bar{\beta}} = - \frac{\partial X}{\partial \mu} \frac{(b + \gamma)}{\alpha(1 + cH)^2} \quad (\text{A.5})$$

$$\frac{\partial}{\partial q} \frac{\partial \alpha}{\partial \bar{\beta}} = - \frac{\partial X}{\partial q} \frac{(b + \gamma)}{\alpha(1 + cH)^2} \quad (\text{A.6})$$

$$\frac{\partial}{\partial b} \frac{\partial \alpha}{\partial \bar{\beta}} = - \frac{\partial X}{\partial b} \frac{(b + \gamma)}{\alpha(1 + cH)^2} + \frac{X}{\alpha} \quad (\text{A.7})$$

$$\frac{\partial}{\partial \gamma} \frac{\partial \alpha}{\partial \bar{\beta}} = - \frac{\partial X}{\partial \gamma} \frac{(b + \gamma)}{\alpha(1 + cH)^2} + \frac{X}{\alpha}, \quad (\text{A.8})$$

where equations (A.4-A.8) are all evaluated at $\beta = \bar{\beta} = \beta^*$.

From equation (A.3) it is clear that $\frac{\partial}{\partial c} \frac{\partial \alpha}{\partial \bar{\beta}}$ is sign-equivalent to $-\frac{\partial X}{\partial c}$. Analysis indicates that $\frac{\partial X}{\partial c} > 0$ for a wide range of random parameter values and it therefore follows that $\frac{\partial}{\partial c} \frac{\partial \alpha}{\partial \bar{\beta}} < 0$, see *main text* figure 1a. Similarly this holds for host reproduction, a .

From equation (A.5) it is clear that $\frac{\partial}{\partial \mu} \frac{\partial \alpha}{\partial \bar{\beta}}$ is sign-equivalent to $-\frac{\partial X}{\partial \mu}$. Analysis indicates that $\frac{\partial X}{\partial \mu} < 0$ for a wide range of random parameter values and it therefore follows that $\frac{\partial}{\partial \mu} \frac{\partial \alpha}{\partial \bar{\beta}} > 0$, see *main text* figure 2c. Similarly this holds for crowding, q .

From equation (A.7) it is clear that $\frac{\partial}{\partial b} \frac{\partial \alpha}{\partial \bar{\beta}} > 0$ when $\frac{\partial X}{\partial b} < 0$. Analysis indicates that $\frac{\partial X}{\partial b} < 0$ for a wide

range of random parameter values and it therefore follows that $\frac{\partial}{\partial b} \frac{\partial \alpha}{\partial \beta} > 0$, see *main text* figure 2b. Similarly this holds for recovery, γ .

Finally, since α is an increasing function of β , $\frac{\partial}{\partial b} \frac{\partial \alpha}{\partial \beta} > 0$ implies that the trait value at the CSS will increase with an increase in b (this holds for all of the above parameters).

Appendix B Parasite virulence in the non-seasonal *DDV* model cannot branch

For the trait to branch the singularity must be convergent stable (CS) and not evolutionarily stable (non-ES). The combination of these conditions results in the requirement,

$$\left. \frac{\partial^2 r}{\partial \bar{\beta} \partial \beta} \right|_{\bar{\beta}=\beta=\beta^*} = \left(\frac{\partial X}{\partial \beta} - c\alpha'(\bar{\beta}) \frac{\partial H}{\partial \beta} \right) \Big|_{\bar{\beta}=\beta=\beta^*} < 0 \quad (\text{B.1})$$

$$\Leftrightarrow \left. \frac{\partial H}{\partial \beta} \frac{b + \gamma}{\beta(1 + cH)} \right|_{\bar{\beta}=\beta=\beta^*} > 0, \quad (\text{B.2})$$

where the invasion fitness, r , is given by equation (5) - *main text*. Equation (B.2) follows by combining the derivative of the equilibrium solution of equation (2) - *main text* with respect to β (i.e. $\frac{\partial}{\partial \beta} (\frac{1}{Y} \frac{dY}{dt}) = 0$), equation (B.1) and equation (6) - *main text*. Thus branching is only possible when,

$$\frac{\partial H}{\partial \beta} > 0. \quad (\text{B.3})$$

The derivatives of the endemic equilibria with respect to β are related according to,

$$\frac{\partial Y}{\partial \beta} = \frac{b + \mu}{b + \mu + \gamma} \frac{\beta - c\alpha}{c\alpha} \frac{\partial X}{\partial \beta} \quad (\text{B.4})$$

$$\frac{\partial Z}{\partial \beta} = \frac{\gamma}{b + \mu + \gamma} \frac{\beta - c\alpha}{c\alpha} \frac{\partial X}{\partial \beta} \quad (\text{B.5})$$

$$\frac{\partial H}{\partial \beta} = \frac{\beta}{c\alpha} \frac{\partial X}{\partial \beta}, \quad (\text{B.6})$$

where equation (B.6) follows from differentiating the equilibrium condition of equation (2) - *main text* with respect to β (i.e. $\frac{\partial}{\partial \beta} (\frac{1}{Y} \frac{dY}{dt}) = 0$) and equations (B.4) and (B.5) follow from combining equation (B.6), the equilibrium condition of equation (3) - *main text* and $\frac{\partial H}{\partial \beta} = \frac{\partial X}{\partial \beta} + \frac{\partial Y}{\partial \beta} + \frac{\partial Z}{\partial \beta}$. Hence, the derivatives $\frac{\partial X}{\partial \beta}$, $\frac{\partial Y}{\partial \beta}$, $\frac{\partial Z}{\partial \beta}$, $\frac{\partial H}{\partial \beta}$ are all sign-equivalent.

Differentiating the equilibrium condition of equation (1) - *main text* with respect to β (i.e. $\frac{\partial}{\partial \beta} (\frac{1}{X} \frac{dX}{dt}) = 0$) and substituting in equations (B.4-B.6) leads to,

$$\frac{\partial X}{\partial \beta} \phi = XYc\alpha(b + \mu + \gamma), \quad (\text{B.7})$$

where,

$$\phi = ((a\beta(1 - 2qH) - c\alpha(b + Y\beta))(b + \mu + \gamma) + (\beta - c\alpha)(\mu\gamma - X\beta(b + \mu))). \quad (\text{B.8})$$

The endemic equilibrium point (X, Y, Z) is stable only if the determinant of the Jacobian of the system given

by equations (1 – 3) - *main text* at the endemic equilibrium is negative. It can be shown that this condition implies that,

$$\phi < 0, \tag{B.9}$$

and hence it follows from equation (B.7) that $\frac{\partial X}{\partial \beta} < 0$ and thus $\frac{\partial H}{\partial \beta} < 0$ by equation (B.6). Since this contradicts the branching requirement given by equation (B.3) parasite virulence cannot branch under the assumptions of this model. □

Appendix C Branching in a related *DDV* model

We consider a related *DDV* model with an alternative representation of the virulence component,

$$\frac{dX}{dt} = aH(1 - qH) - bX - \beta XY + \mu Z \tag{C.1}$$

$$\frac{dY}{dt} = \beta XY - (\alpha_0 + \alpha_D H + b + \gamma)Y \tag{C.2}$$

$$\frac{dZ}{dt} = \gamma Y - (b + \mu)Z. \tag{C.3}$$

Here virulence is separated into two components, an adaptive baseline component, $\alpha_0 = \alpha_0(\beta)$, that is present even when there is no density pressure and hence host condition is good, and a density dependent component α_D which is not adaptive with β . There is therefore one cost to being infected which varies with parasite load and another that varies with host condition but not pathogen load.

The invasion fitness is given by,

$$r = \bar{\beta}X - (\alpha_0(\bar{\beta}) + \alpha_D H + b + \gamma), \tag{C.4}$$

with $\bar{\beta}$ representing mutant transmission and the population equilibria taken for resident trait values. The singularity condition is given by,

$$\left(\frac{\partial \alpha_0}{\partial \bar{\beta}} - X \right) \Big|_{\bar{\beta}=\beta=\beta^*} = 0 \tag{C.5}$$

For evolutionary branching to be possible, the system must have mutual invasibility at the singularity, requiring,

$$\left(\frac{\partial^2 r}{\partial \bar{\beta}^2} + \frac{\partial^2 r}{\partial \beta^2} \right) \Big|_{\bar{\beta}=\beta=\beta^*} = \left(-\frac{\partial^2 \alpha_0}{\partial \beta^2} + \bar{\beta} \frac{\partial^2 X}{\partial \beta^2} - \alpha_D \frac{\partial^2 H}{\partial \beta^2} \right) \Big|_{\bar{\beta}=\beta=\beta^*} > 0 \tag{C.6}$$

$$\Leftrightarrow \left(\frac{\partial^2 \alpha_0}{\partial \bar{\beta}^2} - 2 \frac{\partial X^*}{\partial \beta} \right) \Big|_{\bar{\beta}=\beta=\beta^*} < 0, \tag{C.7}$$

where equation (C.7) follows by differentiating the equilibrium condition of equation (C.1) twice with respect to β (i.e. $\frac{\partial^2}{\partial \beta^2}(\frac{1}{X} \frac{dX}{dt}) = 0$) and combining with equation C.6. Additionally for branching the singularity must

not be ES, requiring,

$$\left. \frac{\partial^2 r}{\partial \beta^2} \right|_{\bar{\beta}=\beta=\beta^*} = - \left. \frac{\partial^2 \alpha_0}{\partial \beta^2} \right|_{\bar{\beta}=\beta=\beta^*} > 0, \quad (\text{C.8})$$

therefore if $\frac{\partial X}{\partial \beta} < 0$, then the mutual invasibility condition given by equation (C.7) is satisfied whenever evolutionary stability is violated.

Differentiating and combining the equilibrium conditions of equations (C.1-C.3) with respect to β yields the same relations as equations (B.4-B.6) but this time with $c\alpha = \alpha_D$,

$$\frac{\partial Y}{\partial \beta} = \frac{b + \mu}{b + \mu + \gamma} \frac{\beta - \alpha_D}{\alpha_D} \frac{\partial X}{\partial \beta} \quad (\text{C.9})$$

$$\frac{\partial Z}{\partial \beta} = \frac{\gamma}{b + \mu + \gamma} \frac{\beta - \alpha_D}{\alpha_D} \frac{\partial X}{\partial \beta} \quad (\text{C.10})$$

$$\frac{\partial H}{\partial \beta} = \frac{\beta}{\alpha_D} \frac{\partial X}{\partial \beta}. \quad (\text{C.11})$$

As per Appendix B substitution of equations (C.9-C.11) into the equation given by differentiating the equilibrium condition of equation (C.1) with respect to β (i.e. $\frac{\partial}{\partial \beta}(\frac{1}{X} \frac{dX}{dt}) = 0$) yields,

$$\frac{\partial X}{\partial \beta} \phi = XY \alpha_D (b + \mu + \gamma), \quad (\text{C.12})$$

where,

$$\phi = ((a\beta(1 - 2qH) - \alpha_D(b + Y\beta))(b + \mu + \gamma) + (\beta - \alpha_D)(\mu\gamma - X\beta(b + \mu))), \quad (\text{C.13})$$

and the condition that the determinant of the Jacobian of the system given by equations (C.1-C.3) must be negative in order for the endemic equilibrium to be stable implies that,

$$\phi < 0, \quad (\text{C.14})$$

and hence it follows from equation (C.12) that $\frac{\partial X}{\partial \beta} < 0$ for this model.

Thus the mutual invasibility condition given by equation (C.7) is always met for this model when evolutionary stability is violated (i.e. when equation C.8 is satisfied). When the singularity is additionally convergent stable branching can occur. We have confirmed that branching occurs using simulations of the evolutionary process. □

Appendix D Proof that the CSS position is unaffected by seasonality in the basic *SIRS* model.

The basic *SIRS* model corresponds to equations (1 – 3) - *main text* when $c = 0$. When the dynamics are periodic the invasion fitness of the system over a period from P_0 to P_1 is:

$$r = \frac{1}{T} \int_{t=P_0}^{t=P_1} (\bar{\beta}X(t) - (\alpha(\bar{\beta}) + b + \gamma))dt, \quad (\text{D.1})$$

where $\bar{\beta}$ denotes the mutant transmission rate and X is the equilibrium susceptible density at the endemic steady state of the SIR system which depends on the resident trait β .

Integrating both sides of the infecteds ODE, equation (2) - *main text*, over the period from P_0 to P_1 gives,

$$\int_{t=P_0}^{t=P_1} \frac{\dot{Y}(t)}{Y(t)} dt = \int_{t=P_0}^{t=P_1} (\beta X(t) - (\alpha + b + \gamma))dt \quad (\text{D.2})$$

$$\Leftrightarrow [\ln Y(t)]_{t=P_0}^{t=P_1} = \int_{t=P_0}^{t=P_1} (\beta X(t) - (\alpha + b + \gamma))dt, \quad (\text{D.3})$$

and since $Y(P_1) = Y(P_0)$ the average susceptible density is conserved as follows,

$$\frac{1}{T} \int_{t=P_0}^{t=P_1} X dt = \frac{(\alpha + b + \gamma)}{\beta}. \quad (\text{D.4})$$

Substituting the above expression into the invasion fitness, equation (D.1), yields,

$$r = \frac{\bar{\beta}}{\beta} (\alpha(\beta) + b + \gamma) - (\alpha(\bar{\beta}) + b + \gamma). \quad (\text{D.5})$$

Since this expression does not depend on the amplitude of seasonality, δ , (or either the forcing period, ϵ , or the period of the dynamics, T) the evolutionary steady state equation ($\frac{\partial r}{\partial \beta}|_{\bar{\beta}=\beta=\beta^*} = 0$) will also be independent of δ (and ϵ , T). The CSS values (β^* , α^*), therefore, will not vary with the amplitude or period of seasonality. There is an analogous proof for the case of chaotic dynamics. □

Appendix E Models displaying invariance of evolutionary attractor under seasonality.

The property that evolved virulence is invariant under increased seasonality of forced parameters for a virulence transmission trade-off can be found for a variety of models and a variety of forced parameters.

In the basic *SIRS* model the parameters a , μ , q and β (and combinations of them) can be forced without altering the evolutionary end-point of virulence. We have shown that this is true for a in Appendix D. In the case of μ and q the argument is identical to Appendix D as neither parameter appears in the infecteds ODE (equation 2 - *main text*).

In the case of β , the invasion fitness again is equation (D.1) which now includes a time dependence in the β

term. Averaging the infecteds equation yields,

$$\int_{t=P_0}^{t=P_1} \beta X dt = T(\alpha + b + \gamma) \quad (\text{E.1})$$

$$\Leftrightarrow \frac{1}{T} \int_{t=P_0}^{t=P_1} g(t) X dt = \frac{(\alpha + b + \gamma)}{\beta_0}, \quad (\text{E.2})$$

where the latter equation follows from the definition of forced transmission, $\beta = \beta_0 g(t)$. Substituting this equation (E.2) into the invasion fitness leads to,

$$r = \frac{\bar{\beta}_0}{\beta_0} (\alpha(\beta) + b + \gamma) - (\alpha(\bar{\beta}) + b + \gamma) \quad (\text{E.3})$$

which is not dependent on the amplitude of forcing, δ , or on the period of the forcing, ϵ , or on the period of the dynamics, T . The remaining parameters, however, α , b and γ , result in a time dependent invasion fitness when they are forced.

Therefore, for *SIRS* type models, forcing of any parameter that does not govern the infectious period has no impact on the evolutionary endpoint of parasite virulence. The result, however, does not generally extend to models with an exposed class [1].

References

- [1] Bacaër, N. 2007 Approximation of the basic reproduction number R_0 for vector-borne diseases with a periodic vector population. *Bull. Math. Biol.* **69**: 1067–1091.